PAN-PACIFIC ENTOMOLOGIST
68(4): 261–267, (1992)

COPULATORY COURTSHIP AND NOTES ON THE NATURAL HISTORY OF *OCHTHERA OCCIDENTALIS* CLAUSEN (DIPTERA: EPHYDRIDAE)

WILLIAM G. EBERHARD
Smithsonian Tropical Research Institute and
Escuela de Biología, Universidad de Costa Rica,
Ciudad Universitaria, Costa Rica

Abstract.—Male *Ochthera occidentalis* court females both before and during copulation. The raptorial forelegs, which are relatively longer in males than in females, are used in aggressive displays.

Key Words.—*Ochthera occidentalis,* ephydrid fly, copulatory courtship, behavior, sexual selection

Male courtship behavior is generally thought to occur prior to genitalic coupling, and to function to induce the female to allow the male to copulate with her. Recent studies have shown, however, that courtship also frequently occurs *during* (and sometimes after) copulation ("copulatory courtship") (Eberhard 1991). The existence of copulatory courtship implies that selection has favored male abilities to induce females to perform post-intromission processes that increase their chances of fertilizing her eggs (Eberhard 1991; see also Otronen & Siva-Jothy 1991, von Helversen & von Helversen 1991). The existence of selection favoring copulatory courtship is of theoretical importance, in particular because a general theory of the evolution of animal genitalia (Eberhard 1985) is based on the premise that courtship after intromission has been achieved is common in animals with internal fertilization.

Thus the discovery of copulatory courtship in the ephydrid fly *Ochthera occidentalis* Clausen is of interest. The genus *Ochthera* is unusual in that both sexes have enlarged raptorial forelegs (Clausen 1977, 1980), which they use both as predatory and signalling devices (Deonier 1974, Simpson 1975). The adults are commonly found along mud or sand shores, or in swampy areas (Simpson 1975). This note describes the sexual behavior of *O. occidentalis* and other aspects of its natural history.

STUDY SITE AND METHODS

Observations were made on a cloudy day at the muddy edge of a shallow pool of brackish water on 8 Sep 1989 near Chamela, Jalisco, Mexico. I observed the flies by lying flat, so that my face was less than 18 cm from the surface of the mud and between 18 and 60 cm from the flies. All observations were in the approximately 0.5 m^2 area visible just in front of me as I lay still. There were generally 10–30 flies in this area at any given moment. This area was part of a small cove about 10 m across. Because major movements of my body disturbed the flies, some observations were recorded only after a behavioral sequence had ended, and approximate times of under 30 sec were estimated by counting off seconds; longer times were determined using a watch. Not all behavioral patterns were checked during each interaction, so sample sizes for different patterns differ.

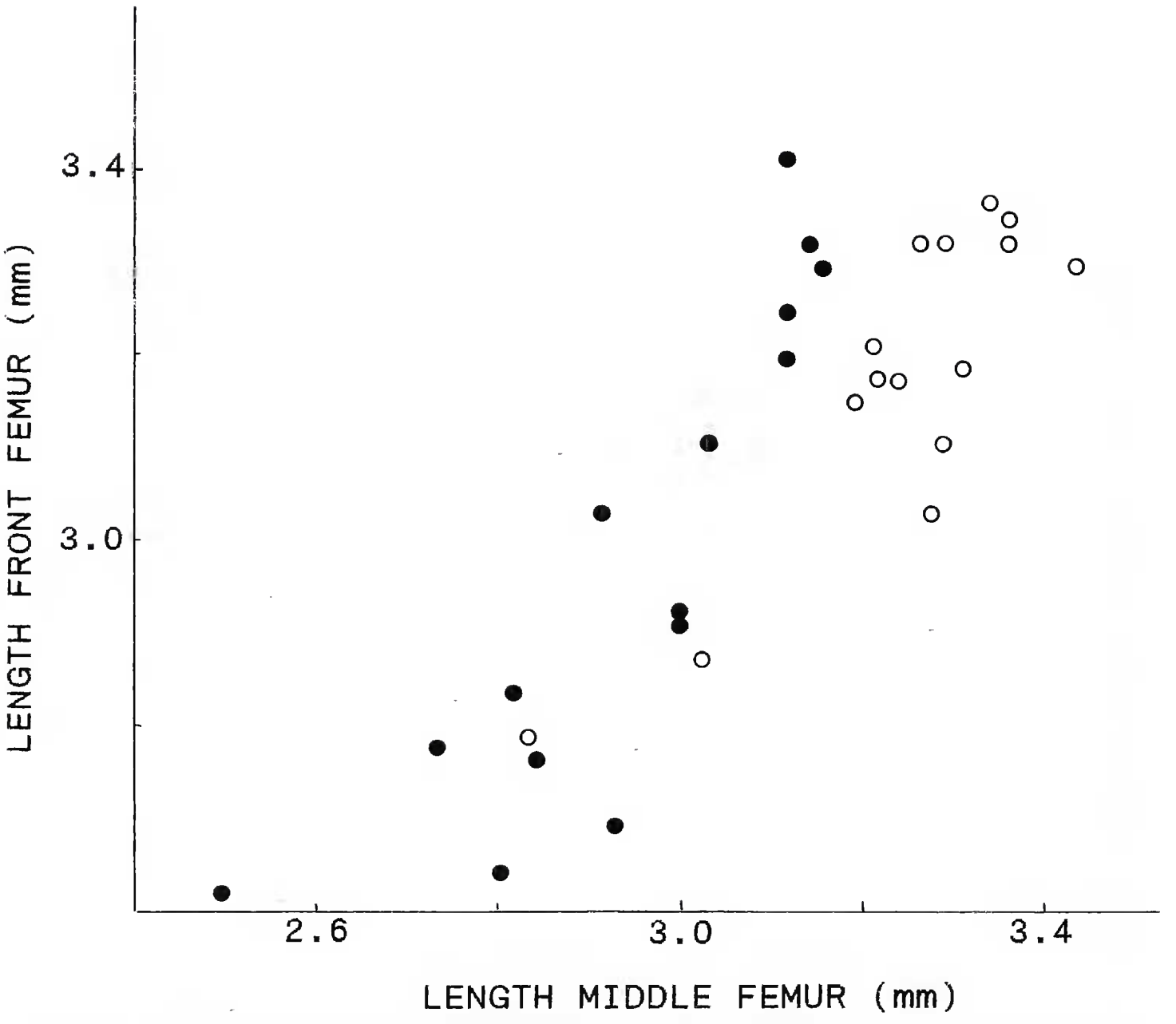

Figure 1. Relation between length of middle and front femur in 15 males (dark circles) and 15 females (open circles) of *O. occidentalis*. The males tended to be smaller, but had front femora of proportionally larger size.

Males and females could not be distinguished reliably in the field on the basis of their morphology. The sex of some individuals was established, however, on the basis of their behavior (males identified on the basis of having mounted another fly, females on the basis of having been mounted and copulated); by following the activity of these individuals it was possible to determine the sex of individuals performing some types of behavior.

Results

Sex Differences in Morphology.—Males at the study site differed from females in having a series of strong setae on the ventral surface of the hind femur. Males were somewhat smaller than females (mean head width was 2.71 ± 0.14 mm in males, and 2.89 ± 0.10 in females) ($P = 0.001$ with Kolmogorov-Smirnov Test). Male front femora were proportionally longer than those of females (Fig. 1) ($P = 0.028$ with Kolmogorov-Smirnov Test comparing ratios of front and middle femora of males vs. females). Both sexes had dense pads of hairs on their hind basitarsi.

General Activity.—Most flies were more or less continuously active, walking over the surface of the mud with their bodies held more or less horizontal, tapping

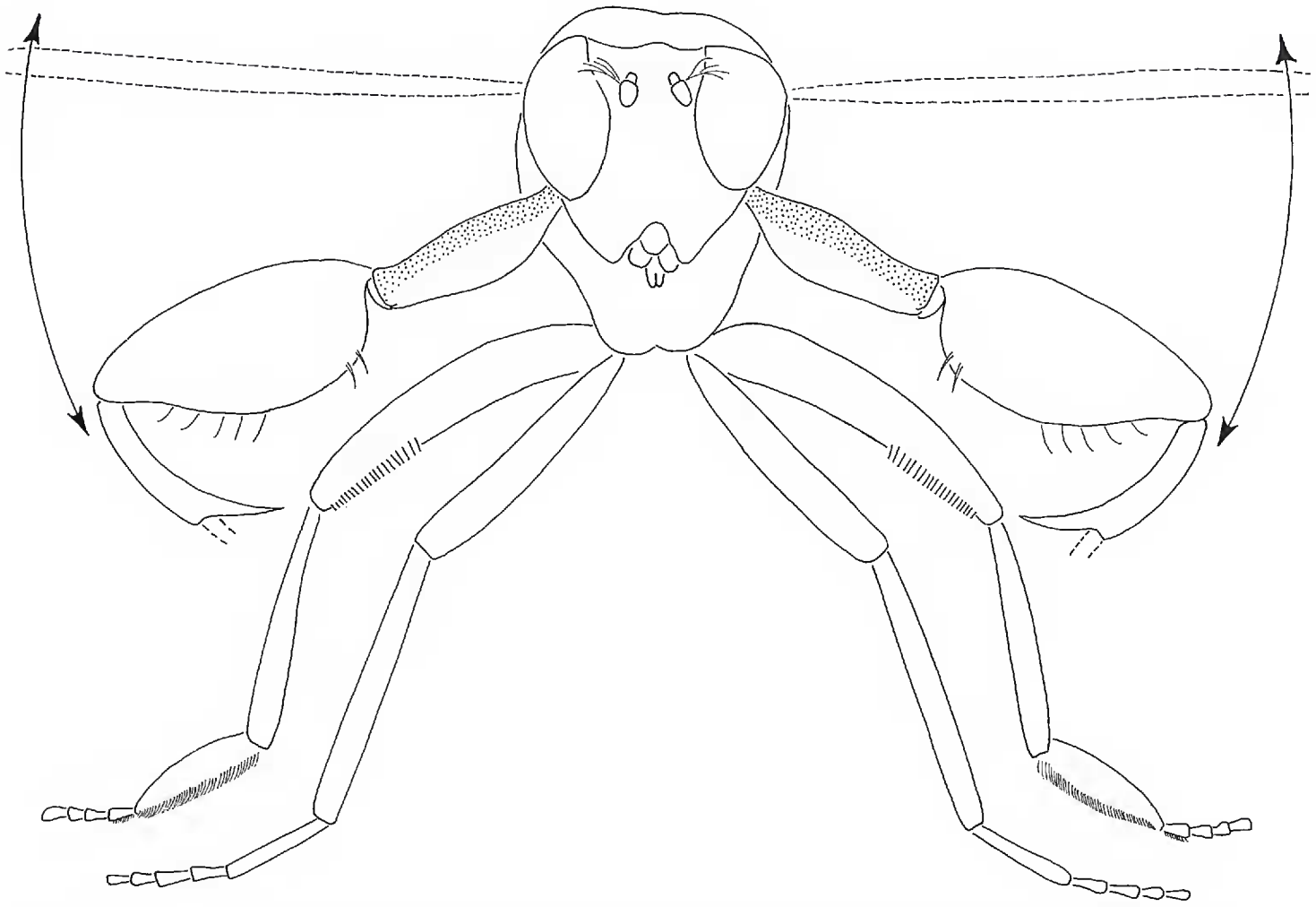

Figure 2. Stylized drawing of a male *O. occidentalis* with its forelegs spread to perform a vibration threat movement (arrows). Positions of front tarsi were not determined, and the tarsi are thus omitted. Stippled areas on front coxae are areas of silvery pile; in life the rest of the front coxae, femora, and tibiae are jet black. The wings (dashed lines) were sometimes vibrated during these displays.

rapidly up and down with their partially extended forelegs. A few paused immobile for several minutes at a time, with their bodies directed upward at about 30° with horizontal. Occasionally they flew, but usually only when frightened by my movements.

Aggressive Interactions.—Aggressive behavior began when one individual turned toward another nearby, and (usually) spread one or both wings. The forelegs were also spread horizontally so the shiny patch of white hairs at the base of the coxae and the flat, black prolateral surfaces of the expanded femur were directed toward the other individual (Fig. 2). The forelegs were waved up and down (Fig. 2), and also partially opened and closed. If the other individual moved away, the aggressor sometimes followed behind for a short distance. Threats of this sort were performed both to other *O. occidentalis* flies, and to much larger cicindellid beetles and saldid bugs.

Sometimes a threatened fly responded with a threat of its own. The two flies moved together until they stood head to head, each with its forelegs spread laterally. Both vibrated their forelegs up and down very rapidly, keeping them in the spread position. Often one or both also spread its wings and buzzed them. Sometimes the flies also pushed against each other with their heads. After no more than 1–2 sec, one of the flies walked or flew away, sometimes pursued briefly by the other.

Aggressive interactions were very common. Some males which were observed for 1–2 min seemed to be especially aggressive, either threatening or courting

every fly they encountered. Such males consistently caused other flies to withdraw. They did not, however, defend any specific site, but instead wandered slowly over the surface of the mud along with the rest of the flies. Quantitative data were not taken, but it appeared that females, at least just after copulating (when I was able to determine their sex), were less aggressive than males, although they also waved their forelegs aggressively.

Precopulatory Courtship.—Males sometimes jumped onto females' backs without any preliminary interaction. More often, however, a male followed behind a female for up to several seconds, keeping his body's long axis parallel to hers and his head about one to two head lengths behind the tip of her abdomen. His forelegs extended forward and vibrated rapidly up and down. The tips of the male's front tibiae or his front tarsi probably contacted the female's abdomen during these vibrations, but I was unable to confirm this. The male moved briskly to maintain his orientation and distance as the female moved and turned. Occasionally such a following male made an apparent attempt to stop the female by moving quickly in front of her, turning toward her and waving his front legs (females sometimes stopped moving forward when a male did this). The male then moved behind her again and resumed foreleg vibrations.

Mounting and Copulation.—In the next stage in courtship, the male jumped onto the female's back, always from the rear. Nearly always the female immediately swung her body violently from side to side in an apparent attempt to dislodge the male. There were additional rapid movements at this time, but the only one I was able to decipher was that the female usually (perhaps always) clawed at the fly on her back by reaching up and backward with her forelegs.

The female usually succeeded in displacing the male, and moved on, with the male either being left behind or following again at her rear, vibrating his forelegs. If the male was not dislodged within a second or two, the female became quiet. Other than brief turns toward approaching flies or other insects, and occasional waves of her forelegs, the female did not move during the rest of the time the male was mounted.

Once a female that had been mounted became quiet, the overall sequence of behavior was the same (19 cases observed carefully). The male immediately began rubbing her with his hind legs, using brief bursts of very rapid movements which lasted approximately 1 sec, interspersed with pauses which lasted on the order of one to several sec. The female's wings were slightly spread so that the tips of the male's hind tibiae and his hind tarsi touched the dorsal surface of her abdomen. Rubbing was performed on the dorsal and lateral portions of the posterior one quarter of the female's abdomen; contact was also made with the posterior margins of the female's wings. Each time the male began to rub, he raised his abdomen slightly, producing a small space between his abdomen and that of the female. The male's forelegs were folded against the anterior portion of his body, apparently out of contact with the female. Mounted males were never attacked or even threatened by other flies, although in a few cases another male vibrated his forelegs rapidly for less than a second at the rear of the female. A female with a mounted male was apparently less likely to flee when I moved than were other nearby flies, but females sometimes flew up to 2–3 m with a riding male when disturbed.

After 150–210 sec ($n = 3$), the mounted male always (19 of 19 cases) moved slightly posteriorly on the female and lowered the tip of his abdomen, and coupled his genitalia with hers. Genitalic coupling lasted an average of 23 $\pm$ 6 sec ($n =$

12). During this time the male always (15 of 15 cases checked for this detail) rubbed intermittently on the dorsal surfaces of the distal portions of the female's wings with his hind tarsi. The rubbing movements were similar to those of abdominal rubbing, but were less vigorous and perhaps also less rapid. In the latter part of copulation pauses between bursts of rubbing were shorter, with the male rubbing almost continuously.

During the last 2–4 sec of genitalic coupling, the female often (9 of 10 cases checked for this detail) waggled her abdomen. These movements were less energetic than those when a male first mounted. The male, perhaps in response to the waggling, dismounted by stepping backward. On several occasions, it was clear that his genitalia remained attached to hers after he stepped back, so that his abdomen was briefly bent forward under his body until uncoupling occurred. There were no further interactions, and the male immediately began moving his front legs and walked away. The female generally stood and groomed for several seconds, then also moved away.

A female that had just mated was often investigated by other flies which turned away immediately after brief contact with the tip of her abdomen. Occasionally, however, a male began following her, vibrated his forelegs and attempted to mount. None of the observed attempts was successful. It seems likely, however, that females do remate, and probably often, given the limited numbers of females present in the cove, the infrequency with which they flew away, and the substantial number of copulations I observed. One female that I followed for 5–10 min after a copulation ate three different prey, was approached and then immediately deserted by seven other flies, and was followed at least briefly with foreleg vibrations by seven others.

Feeding.—Flies moving across the mud tapping with their forelegs occasionally paused and touched the substrate with their mouthparts for approximately 1 sec. Usually I could not see that they obtained food in this way, but on two occasions a fly pulled a shining yellow cylindrical object (probably an insect larva) out of the mud as it raised its mouthparts. These larvae were approximately one quarter of the volume of the fly's head. These and four other food items were supported near the mouth by the prolateral surfaces of the front femora. None of the food items was identifiable, other than an adult ceratopogonid fly that I succeeded in collecting. In one case, a fly ate part of a yellow "larva" and then dropped it and moved away.

Oviposition.—At least five different flies performed what appeared to be oviposition. With the tip of the abdomen pressed to the mud, the fly vibrated its entire body forward and backward very rapidly for about 1–2 sec. Toward the end of this period the fly also rapidly scraped its hind tarsi on the mud, apparently pushing material toward the point where its abdomen touched the mud. Other flies passing near ovipositing individuals neither courted nor threatened them. After an oviposition, the fly moved away, and did not oviposit in the next few minutes.

Discussion

Female rejection of males was much more common than copulation, and overt rejection always occurred before, rather than after, the male began the prolonged and energetic precopulatory rubbing of her abdomen. Thus both this behavior and wing rubbing, which always occurred after the male had achieved intromis-

sion, apparently served to influence female behavior other than initial acceptance of intromission.

Copulatory courtship behavior is different in the other species of *Ochthera* that has been observed. Male *O. mantis* (DeGeer) push intermittently on the substrate with the hind legs during copulation, producing a rhythmic rocking motion of the pair (Simpson 1975), rather than rubbing the female's hind wings as in *O. occidentalis*. Duration of mating is also about ten times longer in *O. mantis* than in *O. occidentalis*. This apparently rapid divergence in copulatory courtship in closely related species is in accord with the hypothesis that it is under sexual selection (Eberhard 1991). Precopulatory courtship also differs between *Ochthera* species. The male of *O. mantis* rubs the female's genitalia for extended periods (Simpson 1975) rather than the dorsal and lateral portions of her abdomen, and prior to mounting males of both *O. mantis* and *O. exculpta* Loew face the female rather than trailing behind her (Simpson 1975).

The functional significance of two secondary sexual structures of males is suggested by the observations reported here. The row of setae on the male hind femur may rake across the posterior edge of the female's wing during precopulatory abdomen rubbing. The relatively longer front femora of males may be related to male–male aggressive displays, in particular the rapid up and down vibrations of front legs during frontal confrontations.

Several observations agree with previous accounts of other *Ochthera* species. In *O. mantis, O. tuberculata* Loew, and *O. exculpta* waving or semaphoring movements of front legs occur in both males and females, and are directed toward both conspecifics and other species (Deonier 1974, Simpson 1975). Waving exposes the fine, silver-colored pile on the inner surfaces of the front legs, including the UV reflective portion of the fore-coxae (Deonier 1974). This behavior has been taken to be courtship (Deonier 1974, Simpson 1975), but the displays by both male and female *O. occidentalis* to species such as cicindellid beetles support a second suggestion by Simpson (1975) that the movements represent threats. Female rejection of mounted males by swinging her body and pushing with her forelegs was similar in *O. exculpta* to that described here for *O. occidentalis*.

Simpson (1975) mentions that conspecific *O. mantis* males sometimes "batter" each other with their forelegs; this may correspond to the rapid up and down vibrations described here. The functional significance of the frequent threat behavior of *O. occidentalis* remains a mystery, since males did not defend either territories or females from other males.

Acknowledgment

I am grateful to Wayne N. Mathis for kindly identifying specimens, and help with literature. Mary Jane West-Eberhard commented on a preliminary version of the manuscript. My trip to Mexico was financed by the Centro de Ecología of the Universidad Nacional Autónoma de México, and my research was supported by the Smithsonian Tropical Research Institute and the Vicerrectoría de Investigación of the Universidad de Costa Rica.

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Received 19 September 1991; accepted 15 January 1992.